

## ***Osmunda cinnamomea* forma *frondosa* at Mountain Lake, Virginia**

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Pronounced dimorphism of sterile and fertile pinnae is a conspicuous morphological attribute of all species of *Osmunda*. Sporangia are borne on the margins of highly reduced segments that lack chlorophyll at maturity. The green spores initially give these fertile pinnae a greenish cast, but after release of the spores, they become wholly cinnamon-brown or gray-brown and soon wither. Of the three *Osmunda* species occurring in eastern North America, two bear fertile pinnae on otherwise undifferentiated sterile fronds: in Royal Fern, *O. regalis* L., these fertile pinnae occur at the leaf tip, while in the Interrupted Fern, *O. claytoniana* L., two to six fertile pinnae occur in the central portion of the frond. In the Cinnamon Fern, *O. cinnamomea* L., the dimorphism is more complete, as sporophylls consist entirely of fertile pinnae and become completely achlorophyllous.

Upon our arrival at Mountain Lake Biological Station in the summer of 1984, we were surprised to discover a large number of *O. cinnamomea* plants bearing partially fertile fronds. These ranged continuously from those which were almost normal, i.e., with only a small portion of sterile blade tissue (usually at the tip) to those which were almost totally sterile, bearing only a few fertile segments, or even simply a few sporangia on sterile segment margins. The distribution of fertile pinnae on the fronds was highly irregular and unpredictable. The most frequent pattern was that with the lower portion of the frond fertile and intergrading into an upper sterile portion (Fig. 1A, B), but numerous fronds were found with a reverse pattern (Fig. 1C), or with sterile pinnae both above and below fertile ones (Fig. 1D). Numerous specimens were taken and have been deposited in the University of Richmond Herbarium.

By midsummer, normal fertile fronds of *O. cinnamomea* wither and fall to the ground or lie draped over sterile leaves. However, the sterile portions of the intermediate leaves remained turgid throughout the summer, making them especially conspicuous (a few of the nearly completely fertile fronds withered). This allowed us to take note of their distribution during our travels in the Mountain Lake area (Giles and Montgomery counties, Virginia) in the summers of 1984 and 1985. It became apparent that the intermediate fronds were very localized; we found them only in the immediate vicinity of the Biological Station and on Bald Knob and Bean Field Mountain near Mountain Lake (about 2 km southwest of the Biological Station). In these areas were patches where the in-



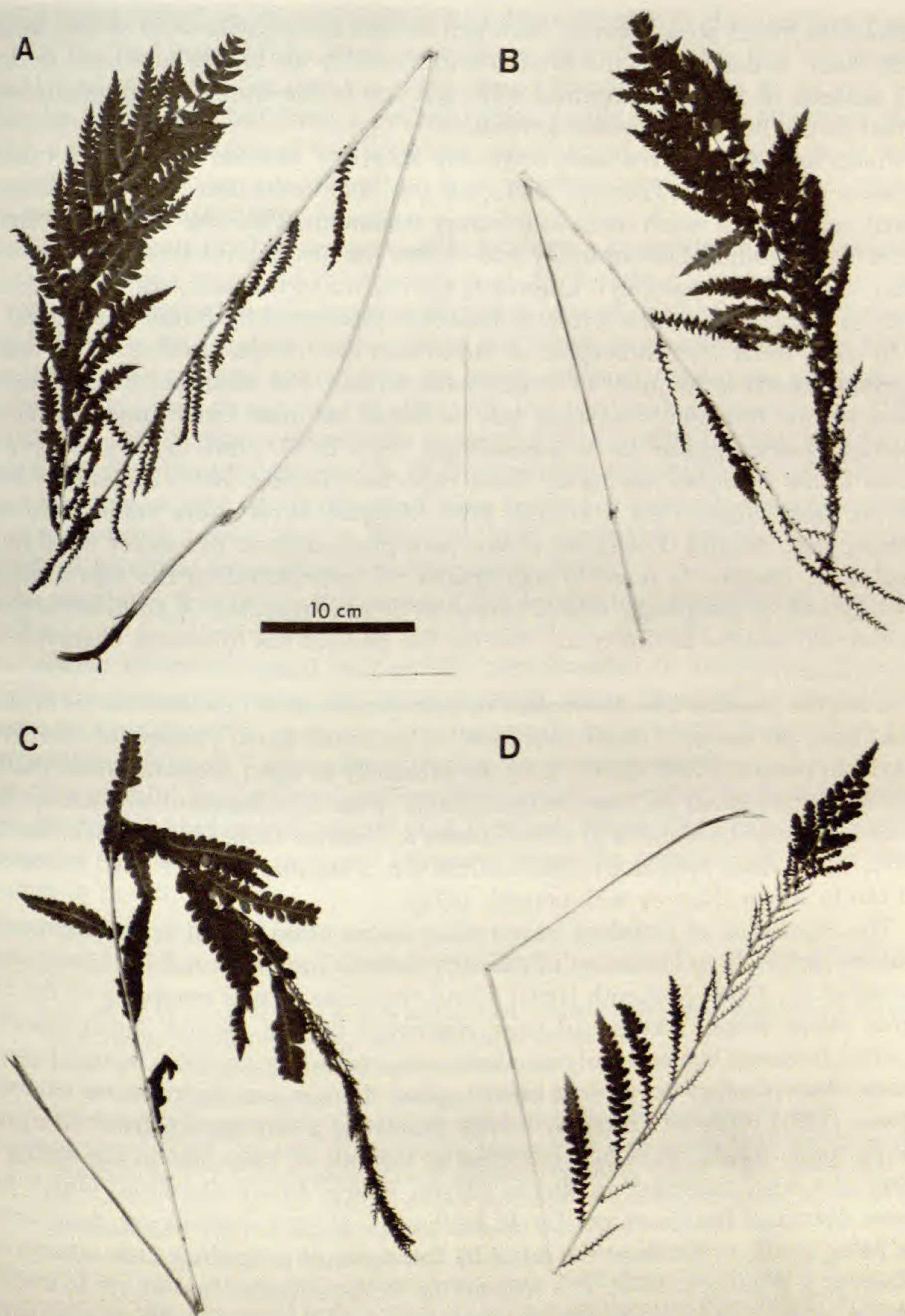


FIG. 1. *Osmunda cinnamomea* forma *frondosa* sporophylls collected at Mountain Lake in the summer of 1984, showing a portion of the range of variation in distribution of fertile pinnae. A and B. Most frequent variant with predominantly fertile lower portion intergrading into predominantly sterile upper portion. C. Leaf with sterile base and fertile tip. D. Leaf with fully fertile area in middle of frond, and with one side more fertile than other.



intermediate fronds predominated, although normal sporophylls were always found with them, sometimes on the same plant. Virtually all leaves produced during the summer of 1985 were normal, although one fertile-tipped intermediate was noted on the Biological Station grounds.

Plants with such leaves were originally accorded varietal status as *O. cinnamomea* var. *frondosa* (Torrey, 1840), but the later reduction to forma (Britton, 1890) represents a much more satisfactory treatment. This leaf form is an environmentally induced abnormality and in this respect is analogous to numerous other trophophyll-sporophyll intermediates known in normally dimorphic ferns such as *Onoclea sensibilis* forma *obtusilobata* (discussed by Beitel et al., 1981).

In some ferns with dimorphic or subdimorphic fronds, production of intermediate fronds is frequent or even characteristic. For example in *Asplenium platyneuron*, intermediate leaves can be found on most individuals. Developmental control appears to be exceedingly rigid in *O. cinnamomea*, however, since forma *frondosa* has rarely been reported (Torrey, 1840; McLouth, 1897; Owen, 1901; House, 1933; Kittredge, 1941; Margaret Wren, pers. comm.; Murray Evans, pers. comm.). The cause of this rare phenomenon has never been fully explained, despite its possible significance in understanding the reproductive biology and/or morphogenesis of leaves in *O. cinnamomea*. A complete explanation will require further study, but for the present the following observations are relevant.

It is quite possible that production of sporophylls in *O. cinnamomea* is dependent upon an elevated nutritional level in the shoot apex. Production of sporophylls in nature is well known to occur primarily in open areas or under partial canopies. Enhanced sucrose concentrations favor development of excised leaf primordia into sporophylls *in vitro* (Sussex & Steeves, 1958; Harvey & Caponetti, 1972, 1973). Also, presence of ammonium ion is required for *in vitro* formation of fertile leaves (Harvey & Caponetti, 1974).

The expression of *frondosa* leaves often seems to be linked to environmental trauma (similarly to formation of partially fertile *Onoclea sensibilis* fronds—see Beitel et al., 1981). McLouth (1897) found *frondosa* fronds emerging in the fall from plants whose leaves had been destroyed by fire. House (1933) reported finding *frondosa* leaves in July on plants surrounded by road tar, though it is not made clear whether the tar had been applied the same or the previous summer. Owen (1901) reported *frondosa* leaves following a late spring frost. Margaret Wren (pers. comm.) collected *frondosa* in the fall of 1980 and in the spring of 1981 at a road construction site in Myrtle Beach, South Carolina, which had been disturbed by Hurricane David in the fall of 1979. Leaves are determined as being sterile or fertile at the latest by the summer preceding their emergence (Steeves & Wetmore, 1953). It is reasonable to hypothesize that injury to trophophylls, which would lower nutrient flow to the shoot apex, might effect a partial reversal in the determination of developing leaf primordia. These altered leaves would then emerge late in the same season or the following spring.

Steeves (1959) hypothesized that a reversal from sterile to fertile condition resulted in the predominantly fertile-tipped fronds observed by himself and by



Torrey (1840), based on the assumption that determination is directed from base to tip of the leaf primordium (Steeves & Briggs, 1958). Extending this hypothesis would lead us to predict that the leafy-tipped fronds observed by us and by Kittredge (1941) resulted from a reversal from fertile to sterile. However, the highly varied distribution of fertile pinnae we observed casts some doubt on this simplified explanation. It is difficult to conceive what sort of stimulus could cause reversals in both directions.

We are currently unable unequivocally to identify an environmental stimulus which might have triggered the formation of the *frondosa* leaves we observed in 1984 at Mountain Lake. A weather station is located on the Biological Station grounds only a few meters from some of the plants in question. Records from this station over several years show no highly unusual conditions, although a cold snap *did* occur in late May of 1984 with low temperatures recorded at 31°F (-1°C). We would like to suggest the possibility that grazing by deer may have been a cause. Substantial grazing on *O. cinnamomea* was observed in the Mountain Lake area in 1982 (W. H. Wagner, pers. comm.). It is possible that instances of severe grazing during 1982 or 1983 may have resulted in the highly localized pattern of *frondosa* occurrence we observed in 1984.

The possibility that injury is a cause of this interesting phenomenon suggests that it may be an adaptive response. A reduction in the amount of photosynthetic area caused by injury could be partially compensated by conversion of presumptive sporogenous tissue into photosynthetic tissue. It would be interesting to attempt to induce this response experimentally by removing leaves from *O. cinnamomea* plants at various times during the growing season.

We are grateful for facilities and weather records provided by the Mountain Lake Biological Station and would like to thank James Caponetti for helpful comments on the manuscript and Margaret Wren for providing details of her findings in South Carolina.

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## SHORTER NOTES

**Gametophytes of *Equisetum giganteum*.**—In a recent article, Duckett and Pang (*J. Linn. Soc., Bot.* 88:11-34, 1984) claimed that sexual behavior of *Equisetum giganteum* L. was similar to that of the other species of *Equisetum* subg. *Hippochaete*, with homosporous spores producing either antheridial or archegonial gametophytes. The archegonial gametophytes as they age begin to produce antheridial lobes and eventually cease archegonial production. The antheridial gametophytes remain so, or with age and by lamellar proliferation also produce archegonial branches. I had earlier described *E. giganteum* gametophytes as different from those of any other species because they were normally bisexual, that is, simultaneously hermaphroditic, with both gametangia being borne upon the same meristem, rather than having separate antheridial lobes as the sequentially hermaphroditic species do (Hauke, *Beih. Nova Hedwigia* 8:1-123, 1963; *Bull. Torrey Bot. Club* 96:568-577, 1969). On this basis I had classified *E. giganteum* as a distinct section *Incunabula*, and theorized on evolution of heterothallism in *Equisetum*.

Duckett and Pang speculated that my culturing procedure, using mass cultures, resulted in a very rapid shift from female to male, which I then interpreted as simultaneous hermaphroditism, rather than rapid sequential hermaphroditism. They cited a plant in cultivation in the Botanic Gardens, Edinburgh as the source of the spores from which they grew their *Equisetum* gametophytes. I wrote to the Botanic Gardens at Edinburgh requesting a specimen from the plant in question. Dr. C. N. Page was gracious enough to send me a fine specimen of that plant, and noted that it was originally collected in Mexico. Although it is superficially much like *E. giganteum*, the Edinburgh plant is *E. myriochaetum* Schlecht. and Cham. That species has stomata in a single line on each side of the internodal grooves, rather than rows 2 to 4 stomata wide. The branch ridges viewed in profile show a sawtooth pattern rather than a blocky pattern. The stem sheath segments are flattened and green, rather than rounded and light brown. So far as I have seen, all large branched *Equisetum* collections from Mexico are either *E. myriochaetum* or the hybrid *E. × schaffneri*, and *E. giganteum* does not occur in that country.

As *E. myriochaetum* rather than *E. giganteum*, the gametophytes described by Duckett and Pang are in agreement with my (1969) descriptions of that species, and their challenge to my classifications of *Equisetum* subg. *Hippochaete* and my hypothesis of evolution of heterothallism in the genus *Equisetum* is not supported.—RICHARD L. HAUKE Department of Botany, University of Rhode Island, Kingston, RI 02881.